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The key role of inter-row vegetation and ants on predation in Mediterranean organic vineyards

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ABSTRACT

Biodiversity-friendly farming practices are taking centre stage, with herbicide use sparking major public debate on human health. Vegetation cover is increasingly used to enhance agroecosystem biodiversity and functions, providing important ecosystem services like biological pest control. However, further information is required on the relationship between vegetation cover, natural enemies, and pest predation. Using a sentinel prey experiment set up in 26 Mediterranean organic vineyards, we analysed the response of generalist predators, and the associated final predation and dynamics under three inter-row management types: bare soil, one out of two inter-rows vegetated and all inter-rows vegetated. Predation on sentinel prey was monitored on the ground and on the vine trunk throughout the daytime and after a night of exposure. Generalist predator abundance was quantified using pitfall traps. Final sentinel prey predation both on vine trunks and on the ground were significantly higher in fully vegetated vineyards, with a shorter prey survival time than in tilled vineyards. Both diurnal and nocturnal predation were significantly related to increased vegetation cover and richness. Moreover, 96 % of the identified predation events involved ants. We demonstrated the key role of vegetation cover in improving the predation function through a spill-over from the inter-row to the grapevine. Contrary to what is commonly observed in agrosystems, we clearly identified ants as the predominant predator both on the ground and on the vine trunk. Our study has important implications for Mediterranean vineyard management, promoting vegetation as a nature-based solution. Sustainable management of vineyard vegetation favouring the natural predator community may contribute to a reduction in pesticide use and fossil fuel consumption.

1. Introduction

A standard practice in conventional viticulture is the removal of inter-row vegetation using herbicides to reduce weed competition (Winter et al., 2018). However, both farmers and society at large are increasingly aware of the need to move from high-input agriculture towards more environmentally sound and sustainable farming practices. Glyphosate, the most widely used herbicide in agriculture (Benbrook, 2016), represents an emblematic example of the need to change a chemistry-based agricultural paradigm dominant since the 1950s (Pimentel, 1996). In 2017, over 1.3 million Europeans signed a petition calling for a ban on this herbicide. Concern over human and environmental exposure to pesticides has led several European countries such as Germany, France, Italy, Austria and Greece to plan a complete ban on

Glyphosate in the coming years. This growing awareness of the need for successful ecological change in agriculture offers an opportunity to rethink vegetation management and to move towards more sustainable and biodiversity-friendly farming practices. This is particularly relevant in vineyards, a perennial crop system with a high pesticide consumption (Butault et al., 2011).

More sustainable vineyard practices like wider use of vegetated inter-rows remain limited by various constraints, such as potential competition for water, particularly in water-limited regions of the Mediterranean (Celette et al., 2009; Ruiz-Colmenero et al., 2011). However, vegetation cover can directly and indirectly provide several ecosystem services to wine and grape production when managed appropriately (Garcia et al., 2018; Winter et al., 2018). Vegetation cover in vineyards can enhance biological activity (Quecedo et al., 2012;

Buchholz et al., 2017), water infiltration (García-Díaz et al., 2017) and organic matter availability (Ruiz-Colmenero et al., 2011). Maintaining vegetation cover improves soil stabilisation because organic matter stabilises aggregates, and root systems protect the soil (Ruiz-Colmenero et al., 2011). Vegetation cover can also favour beneficial organisms associated with grapevines (Altieri and Letourneau, 1982; Sáenz-Romo et al., 2019b) and supports higher levels of biodiversity (Altieri et al., 2005; Wilson et al., 2017b).

Pest regulation has been identified as another important ecosystem service enhanced by the presence of inter-row vegetation. The pest regulation service has commonly been linked to the abundance of natural enemies, such as generalist predators and parasitoids (Costello and Daane, 1999; Sharley et al., 2008; Hoffmann et al., 2017; Sáenz-Romo et al., 2019b). Predators are typically larger than their prey and, unlike parasitoids, they require more than one prey individual during their development. Generalist predators that feed on a variety of prey, such as leafhoppers, flies and caterpillars, are commonly considered to be poorly effective in pest regulation because their numbers are not sufficient to deal with pest population dynamics (Miñarro et al., 2005). However, generalist predator efficiency may be higher if their abundances are high before the pest invades (Symondson et al., 2002). In the case of such early arrival, they may hamper or even prevent pest invasion.

In vineyards, spiders and predatory beetles, such as Carabidae and Staphylinidae, are among the largest generalist predator groups feeding on pests (Thomson and Hoffmann, 2013; Pfingstmann et al., 2019; Sáenz-Romo et al., 2019b). To a lesser degree, lacewings, hoverflies and thrips have been recorded as vineyard predators (Costello and Daane, 1999; Hoffmann et al., 2017; Loni et al., 2017). Although ants are known to favour aphids and coccids through mutualistic interactions (exchanging honeydew for protection, Mansour et al. (2012); Beltrà et al. (2017)), they may also act as predators of insect pests (Offenberg, 2015). All these taxa play a significant role in crop pest regulation (Symondson et al., 2002) and have been shown to be promoted by vegetation cover in vineyards (Thomson and Hoffmann, 2009; Sáenz-Romo et al., 2019a). Vegetation may also facilitate grapevine access to ground-dwelling predators (Frank et al., 2007; Irvin et al., 2016).

In general, the abundance of natural enemies is higher in more diverse ecosystems because vegetation cover provides both additional habitat and food (Nicholls et al., 2000). However, there have been few attempts to document how vegetation cover enhances predation. The relationship between predation and vegetation cover has been explored in several recent studies, but with contrasting results. While Rusch et al. (2017) did not record any direct influence of local vegetation management on pest predation, both native and introduced vegetation cover were found to increase sentinel egg predation in other studies (Danne et al., 2010; Hoffmann et al., 2017). Further investigations are required to improve our understanding of vegetation management effects on both generalist predator abundance and their predatory activity.

Although vegetation cover may help increase generalist predator abundances, predators must move from the inter-row to the grapevine to affect pest insect control. In the present study, we evaluated the abundance of generalist arthropod predators and the related predation function in Mediterranean organic vineyards under three different inter-row management systems. Our predation survey was performed both throughout the day and at night's end, to analyse the effects of vegetation cover, plant species richness and diversity on predators and on the attack on sentinel prey. We addressed the following research questions: (1) Do generalist predator abundance and final predation increase with vegetation cover? (2) Do the effects on predator numbers and final predation depend on vegetation characteristics (plant species richness, percentage of vegetation cover and its variance, beta diversity (Bray-Curtis index)? (3) Are these effects limited to predation in the inter-row, or is there a spill-over effect to grapevine plants? (4) What are the major predator groups attacking sentinel prey?

2. Materials and methods

2.1. Study sites and design

This study was conducted in south-eastern France, between the southern slopes of the Luberon mountains and the Durance river. The landscape is dominated by medium-sized vineyards (0.7 +/- 0.5 ha) and the degree of urbanisation is low. In this region, winegrowers most often keep bare soil from mid-spring to autumn rains. This is the most widely adopted practice. In permanently vegetated vineyards, the vegetation is mowed or laid down before summer. The southern Luberon area has a Mediterranean climate, with hot and dry summers followed by mild winters and irregular precipitation in autumn and/or spring. Mean annual temperatures and total annual precipitation for the period of 2003–2018 are 13.5 °C and 676 mm, respectively.

We selected 26 vineyards involving three different inter-row management types : (i) tillage (0/2) ($N = 8$), (ii) partially vegetated (one out of two inter-rows vegetated) (1/2) ($N = 10$) and (iii) all inter-rows vegetated (2/2) ($N = 8$). All selected vineyards were under organic management, with an average size of 7 008 $\pm$ 746 m^2 and scattered across an area of 20 km by 6 km (Fig. 1). According to the French guidelines for organic viticulture no chemical was applied to the 26 vineyards for at least three years. The inter-rows of all these vineyards were sown at least once in the last five years with commercial grass-legume mixtures. However, with the exception of two vineyards, they were all dominated by spontaneous species (Appendix A). All were planted with either Syrah or Grenache grapevines, the most common varieties in this region.

The lepidoptera *Lobesia botrana* (Lepidoptera: Tortricidae) and the leafhopper *Scaphoideus titanus* (Hemiptera: Cicadellidae) are the main pest insects in the Luberon. The moth *L. botrana* feeds on grapes, reducing yield and increasing susceptibility to fungal infections. *Lobesia botrana* is among the most economically important insects in Europe. *Scaphoideus titanus* is the vector of a phytoplasma that causes the infection by Flavescence dorée. Flavescence dorée causes yield losses and lower grape quality (Chuche and Thiéry, 2014). *Scaphoideus titanus* completes one reproductive cycle in spring and *L. botrana* up to four from early spring to late summer. *Lobesia botrana* larvae can reach a length of 8–9 mm, compared to 3−4 mm for larvae of *S. titanus*.

2.2. Characterisation of vegetation cover and arthropod community

A pair of inter-rows separated by two inter-rows was selected in the centre of each vineyard (Fig. 2). The plant community was recorded in three 2 × 2 m quadrats in each selected inter-row from 13 to 22 May 2019, resulting in a total of six quadrats per vineyard. We identified vascular plant species and estimated their individual percentage cover as well as the total percentage of vegetation cover in each quadrat. Plant percentage cover was estimated as the vertical projection of all above-ground organs. Data were averaged across quadrats within each vineyard.

In order to estimate the most abundant and active predators (Formicidae, Arachnids [spiders, harvestmen] and Carabidae), pitfall traps were placed in two inter-rows in each vineyard and removed after one week. Traps (clear plastic) were 11 cm deep and 8 cm in diameter. They were buried to the rim and filled with propylene glycol to a quarter of the depth. Two pitfall traps were placed 20 m apart in the middle of each of the two inter-rows, resulting in a total of 104 pitfall traps. To avoid an influence of predator trapping on the sentinel prey experiment, the pitfall traps were only placed after the end this experiment in July.

Predatory arthropods were sorted and identified to order for arachnids (Araneae and Opiliones) and to family for Hymenoptera (Formicidae) and Coleoptera (Carabidae) in the laboratory, counted and stored in a 70 % ethanol solution. Our focus being on generalist predators able to prey on larvae at last instar stage, only ground beetles and arachnids larger than 5 mm were considered.
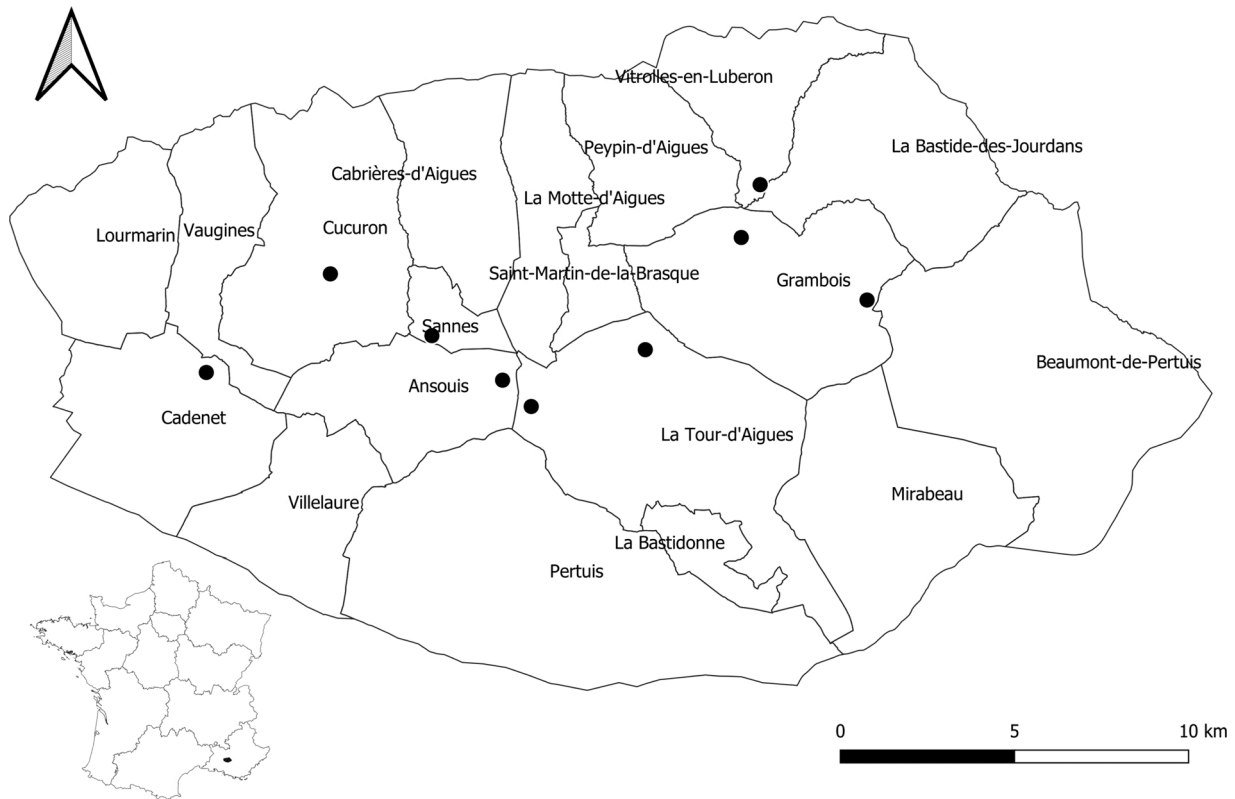
Fig. 1. Position of analysed wineries in the southern Luberon area (south-eastern France). In each winery, one to four vineyards were involved in the study.
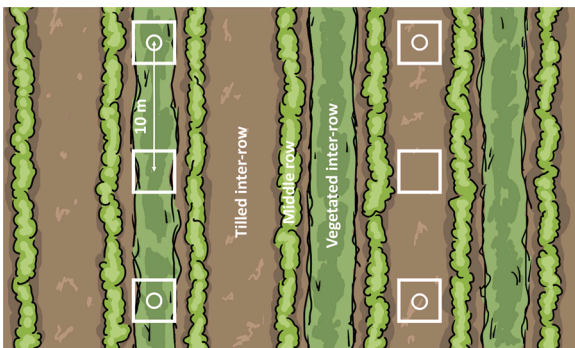

Fig. 2. Example of position of pitfall traps (white circles) and vegetation quadrats (white squares) in a partially vegetated vineyard (1/2).

2.3. Sentinel prey experiment and predator observations

Larvae of *Lucilia* sp. (Diptera, Calliphoridae) were used as sentinel prey to characterise predation by arthropod generalist predators. Sentinel prey can provide a direct, quantitative measure of predation under field conditions. Live sentinel prey provides more realistic data compare to artificial prey (Lövei and Ferrante, 2017). All larvae used for the experiment were at last instar stage, sized ca. one centimetre and white. The sentinel preys were pinned on white cards (2 × 2 cm) for better detection. Forty-eight sentinel cards were placed in each vineyard: 24 per transect, 5 m apart, 12 placed directly on the ground in the middle of the inter-row and 12 attached to the vine trunk about 60 cm high. Cards were placed in the two transects used for vegetation and arthropods sampling. The experiment was conducted over 17 days in June 2019. Observations began at 10 am. The cards were checked four times, after 1, 2, 4.5 and 7 h, and finally removed at 8 pm. New cards were placed in the same position from 9 pm to 8.30 am to assess the level of predation occurring at night. During each survey, we classified the maggots under "presence", "absence" and "attacked". Arthropods eating sentinel preys were visually identified when present. A predation event was recorded if at least one maggot was missing or showed clear signs of attack. Most unattacked larvae remained alive at the end of both exposure sessions.

2.4. Data analysis

Mixed models were computed to explore the effects of management type and vegetation characteristics on different response variables (predator abundance per pitfall trap, final predation (card level), dynamics of predation (survival time) and observations of identified predators (card level)). The vineyard was systematically used as a random explanatory variable. Models were either with management or with vegetation variables. Although vegetation cover and inter-row management are highly correlated, these two approaches are complementary and thus straightforward. Models testing the effect of the inter-row management provide information on impact of agricultural practices and models testing the effect of vegetation variables provide information on biotic interactions between predators and vegetation.

We performed a principal component analysis (PCA) based on (i) mean percentage of vegetation cover and (ii) species richness per quadrat within each vineyard, (iii) within vineyard variance of percentage of vegetation cover across the six quadrats, and (iv) within vineyard beta diversity calculated using the Bray-Curtis dissimilarity index for all pairs of quadrats within vineyards, to reduce the number of vegetation cover variables and to avoid correlation among these variables. We extracted the scores of the first two principal components, PC1 and PC2, which accounted for 45.6 % and 41.2 % of total variance, respectively. The first axis was related to species richness and percentage of vegetation cover, and the second axis was related to beta diversity and variance of percentage of vegetation cover. To facilitate interpretation of the interaction, PC1 and PC2 were considered binary variables.

PCA scores below the mean of all vineyards were transformed to 0 and PCA scores above the mean were transformed to 1.

We first modelled the response of predator abundance in pitfall traps to inter-row management. We conducted these analyses for each predator taxon (ants, spiders, carabids, harvestmen).

Regarding the sentinel prey experiment, a predation event was counted when at least one maggot was missing or showed clear signs of attack. We included the vineyard as a random effect in all analyses of sentinel prey.

Final predation was divided into daytime and night-time events and analysed separately. We used the number of predated larvae as the statistical unit (i.e. the number of larvae attacked or missing from the 48 cards placed in each vineyard). Differences in levels of both diurnal and nocturnal predation according to type of inter-row management were assessed using a GLMM with a binomial distribution and logit link. The card position (ground vs. vine trunk) was added as a fixed explanatory variable. Models included the interaction between inter-row management type and card position. To obtain a better understanding of how the inter-row vegetation parameters affected both diurnal and nocturnal final predation, we applied two separate GLMMs. Both models were run with PC1, PC2 and card position (ground or vine trunk) as explanatory variables and all their possible interactions.

A Kaplan-Meier (Kaplan and Meier, 1958) survival analysis was performed to calculate survival curves, and curves were plotted using the ggsurvplot function of the survminer package. Cox proportional hazard model survival analyses were used to obtain a temporal view of the overall diurnal predation process across the three inter-row management types. The first model related the survival times of sentinel prey to inter-row management type and card position (ground or vine trunk), as well as their interaction, as fixed explanatory variables. The second model related survival times to PC1 and PC2, card position and their interactions. The models were specified using the "coxme" function in R package coxme. Post-hoc tests were run using the emmeans function (emmeans package) to compare the three management types and the two sentinel card positions in cases of significant predictor effects. Finally, we separately explored the effects of inter-row management type and of PC1 and PC2 in interaction with card position on the abundance of individual predator species identified on sentinel prey, using GLMMs with a binomial distribution.

A stepwise selection was employed for model selection using the anova function. Data analyses were performed using RStudio, version 1.2.5033. Packages used here: MASS, glmmTMB, emmeans, survfit, coxme.

3. Results

3.1. Vegetation cover

We recorded 91 plant species in the 0/2 vineyards, predominantly annuals. *Lolium rigidum* (annual), *Convolvulus arvensis* (perennial) and *Avena sterilis* (annual) were the dominant species in the quadrats, with a mean cover of 5.4 %, 1.8 % and 1.7 %, respectively. In the 1/2 vineyards, 115 plant species were sampled, with the dominant species *Lolium rigidum*, *Bromus hordeaceus* and *Vicia sativa* covering 9.2 %, 3.5 % and 3.3 % of the quadrats, respectively. We identified 114 plant species in the 2/2 vineyards. While the vegetation was also dominated by annuals such as *Lolium rigidum*, *Medicago minima*, with a mean cover of 12.1 %, 7% respectively, perennials such as *Lolium perenne* (6.1 %) reached a much higher cover than in the other management types.

3.2. Predator communities

We captured 4 217 predators across the 26 vineyards. Ants were by far the most abundant predators (3 312 individuals), followed by spiders (631), ground beetles (152) and harvestmen (122). We observed an effect of inter-row management type only on ants abundance (Table 1,

Table 1

Effects of inter-row management and vegetation parameters on recorded predator taxa in pitfall traps. PC1 is the PCA first axis related to percentage of vegetation cover and plant species richness. PC2 is the second axis related to beta diversity and vegetation cover variance. The different models are separated by line. Only significant interactions (<0.05) are indicated in the table. Values in bold indicate significant effects at P < 0.05.

Response variables	Explanatory variable	Estimate / Chisq	P-value
Ant abundance	**Management type**	**7.22**	**0.03**
	PC1	3.79	0.05
	PC2	**3.95**	**<0.05**
	Management type	0.15	0.93
Spider abundance	PC1	2.94	0.09
	PC2	0.00	0.98
	PC1*PC2	**7.69**	**0.01**
	Management type	2.03	0.36
Carabidae abundance	PC1	0.14	0.71
	PC2	0.05	0.83
	PC1*PC2	3.81	0.05
	Management type	0.84	0.66
Harvestman abundance	PC1	0.02	0.90
	PC2	0.01	0.93
	PC1*PC2	**7.10**	**0.01**

Appendix B), with nearly 50 % more ants in 2/2 (mean ± se = 47.5 ± 7.92) vineyards than in 0/2 (mean ± se = 24.9 ± 5.49) (P = 0.03). Higher variance in percentage of vegetation cover and beta diversity (PC2) were associated with higher abundances of ants (Table 2). Abundances of both spiders and harvestmen depended on the interaction between PC1 (percentage of vegetation cover and plant species richness) and PC2 (Table 2). When beta diversity and vegetation cover variance were high, spiders were significantly more abundant under a higher percentage of vegetation cover. When beta diversity and vegetation cover variance were low, spiders were more abundant under a lower percentage of vegetation cover.

3.3. Sentinel prey experiment

The probability of larvae being attacked during daytime was significantly affected by inter-row management type, card position, and their interaction (Table 2). Sentinel prey was significantly less attacked in 0/2 vineyards than in 1/2 vineyards when cards were on the ground, and significantly less than in 2/2 vineyards when cards were on the vine trunk (P < 0.004 and P = 0.02 respectively). Larvae located on the ground were significantly more attacked than those on the vine trunk (P = 0.01, P < 0.001 and P < 0.001, respectively for 0/2, 1/2 and 2/2)

Table 2

Summary of the generalized linear mixed-effects models explaining final predation during day and at night. PC1 is the PCA first axis related to percentage of vegetation cover and plant species richness. PC2 is the second axis related to beta diversity and vegetation cover variance. The different models are separated by line. Only significant interactions (<0.05) are indicated in the table. Values in bold indicate significant effects at P < 0.05.

Response variables	Explanatory variables	Chisq	P-value
Diurnal predation	**Management type**	**9.39**	**0.01**
	Card position	**62.74**	**<0.001**
	Management type*Card position	**9.97**	**0.01**
Nocturnal predation	Management type	3.65	0.16
	Card position	**68.90**	**<0.001**
Diurnal predation	**PC1**	**4.95**	**0.03**
	PC2	0.23	0.63
	Card position	**62.80**	**<0.001**
Nocturnal predation	**PC1**	**5.18**	**0.02**
	PC2	0.01	0.92
	Card position	**68.94**	**<0.001**
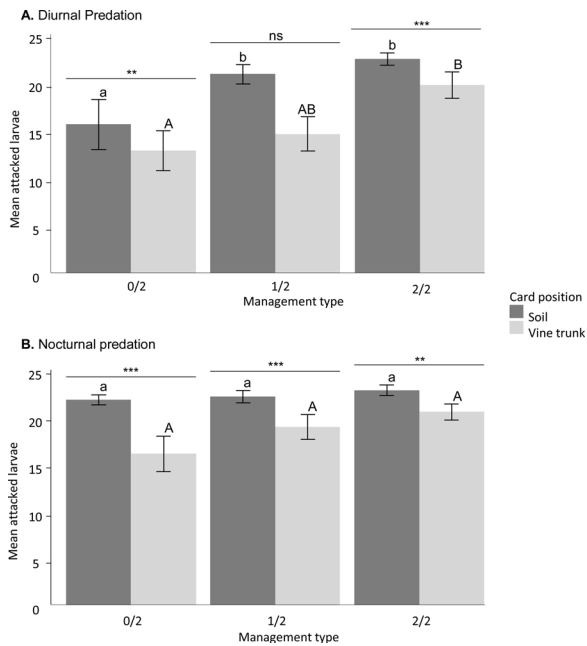
Fig. 3. Mean final predation rates (± SE) on sentinel prey per inter-row management type during day A. and at night B. Different letters indicate significant differences between management types (P < 0.05), capital letters are used to compare observations on the vine trunk and lowercase to compare observations on the ground. Stars are used to compare observations between the two compartments within management types (ns: non-significant; **:P<0.001; ***: P < 0.0001).

(Fig. 3). Only card position affected nocturnal predation (Table 2), and this effect was similar under the three different management types: larvae on the ground were more attacked than those on the vine trunk (0/2 : P < 0.001, 1/2 : P < 0.001 and 2/2 : P = 0.002; Table 2 and Fig. 3). Final predation significantly increased with increasing percentage of vegetation cover and species richness (PC1), both during the day and at night (Table 2).

The Cox-regression revealed a significant interaction between vegetation cover management and card position (Table 3, Fig. 4). Larvae on the ground were more susceptible to predation under all three management types. The predation risk for larvae both on the ground and on the vine trunk was 2.55 and 2.75 times higher in 2/2 than in 0/2 (respectively, P = 0.01 and P = 0.01). There was a significant effect of PC1 (percentage of vegetation cover and species richness), card position and their interaction on the survival time of sentinel prey. PC1 significantly affected the survival time of sentinel prey only on the vine trunk.

Table 3
Effect of inter-row management type and card position and their interaction on survival time of sentinel prey according to the Cox-model. PC1 is the PCA first axis related to percentage of vegetation cover and plant species richness. PC2 was removed following model selection. The different models are separated by line. Only significant interactions (<0.05) are indicated in the table. Values in bold indicate significant effects at P < 0.05.

Response variable	Explanatory variables	Chisq	P-value
Survival time of sentinel prey	**Management type**	**8.07**	**0.02**
	Card position	**40.96**	**<0.001**
	Management type*Card position	**7.54**	**0.02**
	PC1	**4.01**	**<0.05**
	Card position	**40.54**	**<0.001**
	PC1*Card position	**8.94**	**0.003**
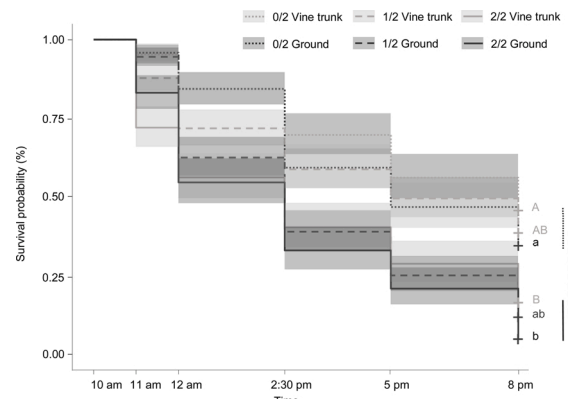
Fig. 4. Effect of management type on survival of larvae (sentinel prey) on the ground and on vine trunk during daytime (Kaplan-Meier method). Different letters indicate significant differences in pairwise comparisons using the Cox-model (P < 0.05). Capital letters are used to compare observations on the vine trunk and lowercase to compare observations on the ground. Stars are used to compare observations between the two compartments within management types (dotted line: tilled vineyards (0/2); dashed line: partially vegetated vineyards (1/2); solid line: fully vegetated vineyards(2/2); (*: P < 0.01; non-significant; ***: P < 0.0001).

3.4. Observed predators

We observed and identified a predator in 80 % of the daytime predation events. Ants represented almost all the observations (96 %), with very limited predation by spiders (2.1 %) and other arthropods (1.9 %). *Cataglyphis cursor* was the most active ant on the ground, whereas *Camponotus vagus* and *Crematogaster scutellaris* were the most active predators on the vine trunk. Inter-row management type, card position and their interaction significantly affected the presence of ants on sentinel cards (Table 4). More ants were observed to attack larvae on the ground than on the vine trunk under 1/2 and 2/2 management types (Appendix C) (P < 0.001 for both). Significantly more larvae were attacked by ants in the 1/2 and 2/2 vineyards than in the tilled vineyards when on the ground (1/2: P = 0.02 and 2/2: P = 0.03). The model exploring the influence of vegetation parameters (PC1 and PC2), card

Table 4
Summary of the generalized linear mixed-effects models explaining observations of ants attacking sentinel prey. Only cards on the ground were considered for *C. cursor* and only cards on the vine trunk were considered for both *C. vagus* and *C. scutellaris*. PC1 is the PCA first axis related to percentage of vegetation cover and plant species richness. PC2 is the second axis related to beta diversity and vegetation cover variance. Only significant interactions (<0.05) are indicated in the table. Values in bold indicate significant effects at P < 0.05.

Response variables	Explanatory variables	Chisq	P-value
Observed ant attacking prey	Management type	4.48	0.11
	Card position	**61.83**	**<0.001**
	Management type*Card position	**9.28**	**0.01**
Observed *C. cursor* attacking prey	PC1	3.27	0.07
	PC2	0.02	0.89
	Card position	**61.83**	**<0.001**
	Management type	**8.90**	**0.01**
Observed *C. vagus* attacking prey	PC1	1.81	0.18
	PC2	0.01	0.93
	Management type	2.50	0.29
Observed *C. scutellaris* attacking prey	PC1	1.18	0.28
	PC2	0.01	0.93
	PC1*PC2	**5.84**	**0.02**
	Management type	4.03	0.13
	PC1	0.30	0.58
	PC2	0.38	0.54

position and their interaction on observations of ants attacking larvae revealed a significant effect of card position only (Table 4).

When the three species were modelled separately, *Cataglyphis cursor* was the only species affected by inter-row management type, attacking larvae more in the vegetated inter-row vineyards (1/2: P = 0.01 and 2/2: P < 0.05). The number of *Camponotus vagus* observations was dependent on the interaction between PC1 and PC2 (Table 4).

4. Discussion

This study reveals a clear positive effect of inter-row vegetation on the predation dynamics and final predation of sentinel prey. Although this effect was more pronounced on the ground, a spill-over from the vegetated inter-rows to the grapevines was observed. We also demonstrate for the first time in temperate perennial crops the predominant role of ants as potential natural enemies of pest insects. Our findings provide valuable insights into the strong functional role that vegetation plays as a driver of predation dynamics.

4.1. Predator response to vegetation cover

The predatory community was dominated by four taxa: ants, spiders, predatory ground beetles and harvestmen. These taxa recognised as generalist predators are commonly found in crop studies (Symondson et al., 2002). Ants were by far the most abundant predators, which is consistent with their ubiquitous occurrence and with other studies capturing ground-dwelling arthropods in Mediterranean vineyards (Hoffmann et al., 2017; Carlos et al., 2019; Sáenz-Romo et al., 2019a). We find a management type effect only on ant abundance which were more abundant in fully vegetated vineyards than in tilled ones, and a response to vegetation parameters concerning PC2. Whereas ants did not significantly respond to the percentage of vegetation cover and species richness, they were less abundant in vineyards with high vegetation cover variance and diversity. Because ant abundance generally increases with an increase in vegetation structure complexity (Ríos-Casanova et al., 2006) and is less affected by plant species composition and richness (Uhey et al., 2020; Andersen, 2019, but see Carlos et al., 2019), we would have expected a positive effect of an increase in variance of vegetation cover. It seems that vegetation structure can modulate ant responses to microclimate, which is a key driver in shaping ant communities (Uhey et al., 2020). An increase in vegetation cover variance may have a global negative effect on the abundance of ants by decreasing soil humidity and increasing soil temperature. This is corroborated by the fact that fully vegetated vineyards, which has the lowest variance of vegetation cover, had almost twice the abundance of ants in 0/2 and 1/2 vineyards. Spiders and harvestmen were also affected by vegetation, their abundance increasing with increased vegetation cover variance and diversity only when vegetation cover and richness were high. While spiders are known to be affected by vegetation cover (Costello and Daane, 1998; Pfingstmann et al., 2019), this effect is less common for harvestmen (Vogelweith and Thiéry, 2017).

4.2. Effects of inter-row vegetation management on predation

Our results show that inter-row management type and percentage of vegetation cover, plant species richness (described by PC1) positively affected sentinel prey predation, in terms of both final predation and predation dynamics. The magnitude of this effect varied over compartments (ground vs grapevine plant) and periods (day vs night).

Overall diurnal attacks on sentinel prey both on the ground and on the grapevine plants increased from non-vegetated to fully vegetated vineyards, as a function of the increasing plant species richness and percentage of vegetation cover. At night, attacks on sentinel prey increased with plant species richness and percentage of vegetation cover but did not respond to inter-row management type. We observed an increase in predation events in both the 0/2 and 1/2 vineyards, which

suggests a change in the predator community, with more predators being active at night. These communities may not respond in the same way to management. There is a scientific evidence that arthropods communities differ between day and night (Petersen and Woltz, 2015). Importantly, the survival time was negatively correlated to vegetation cover indicating that predation events occurred faster in fully vegetated vineyards. A quick response to pest invasion is key to successful management of pest species (Murdoch et al., 1985). A positive relationship has previously been observed between local vegetation and predation occurring on the ground or on the crop (Speight and Lawton, 1976; Danne et al., 2010; Hoffmann et al., 2017). As suggested by Nicholls et al. (2008), non-crop vegetation increases the agroecosystem diversity and complexity providing habitats and resources for beneficial arthropods.

Predation occurring on the grapevine plants is important since predation on the ground does not necessarily provide protection against pest attack. Contrary to the results of Wilson et al. (2017a) not showing any effect on crop pests, we observed a spill-over effect from ground vegetation to vine trunk. Sentinel preys on the trunk were attacked more often in fully vegetated vineyards than in vineyards with bare soil. Irvin et al. (2016) showed that migration of pests and beneficial insects into the grapevine canopy was enhanced by vegetation cover. They suggested that buckwheat is highly attractive to beneficial insects, with a secondary migration from ground vegetation to the crop. Movements from ground vegetation to the canopy of a pear orchard were studied using an immunomarking method (Horton et al., 2009) to determine the possible contribution of vegetation cover to the crop canopy predator community. Their findings confirmed observations by Frank et al. (2007) and Shapira et al. (2018) showing that the community of generalist predators in the crop canopy differs from that of predators in the ground vegetation. These findings may explain the differences between final predation and the survival times of sentinel prey on the ground and on the vine trunk observed in our study. Natural enemies have been found to be more abundant and more active in the ground vegetation than in vine foliage because of its higher diversity of habitats and resources (Frank et al., 2007; Shapira et al., 2017).

4.3. The unexpected role of ants in predation

A positive correlation between non-crop vegetation cover and predator densities and a corresponding negative correlation with pest insect densities have been demonstrated in other studies (Nicholls et al., 2000; Vogelweith and Thiéry, 2017). In our case, the responses of predation and of ant abundance in traps to inter-row management were correlated.

In the almost 80 % of predation events for which we identified a predator preying on larvae, 96 % were ant workers. We observed two different ant communities attacking sentinel prey, one in the inter-rows and the other in the grapevine canopy. Predation events on the ground were dominated by *Cataglyphis cursor,* whereas *Crematogaster scutellaris* and *Camponotus vagus* were the predominant species on the vine trunk. Ants are among the most abundant surface-active arthropods captured in agrosystems (Carlos et al., 2019; Sáenz-Romo et al., 2019a). They have previously been found to attack sentinel prey in orchards and agroforestry systems (Mathews et al., 2004; Martin-Chave et al., 2019), but never in vineyards (Danne et al., 2010). Vineyard inter-rows are more exposed to high temperatures and drought events than orchard inter-rows. In our study, the high abundance of *C. cursor*, a hot climate specialist, is consistent with theses microclimatic differences between vineyards and orchards. The relatively warm and dry conditions of our vineyards may also explain the low abundance of predatory ground beetles commonly found in orchards (Mathews et al., 2004).

Overall predation by ants was affected by inter-row management type and card position. When cards were on the ground, more ants were observed in both types of vegetated vineyards than in non-vegetated vineyards. The surface-active *C. cursor* was the only species that

responded to inter-row management type, with more attacks in the two vegetated management types than in the tilled one. Ants are known to be sensitive to tillage (Sharley et al., 2008), which, together with an increase in available resources, may explain why ground predation increased in vegetated inter-rows whereas vine trunk predation by ants was unaffected by management type. However, more observations of one of the predominant predators on the vine trunk, i.e. *C. vagus,* were made on vine trunks in fully vegetated vineyards (in total, 50 observations of predation events) than in tilled vineyards (in total, 27 observations of predation events). They were influenced by the interaction between PC1 and PC2 (species richness and percentage of vegetation cover, and percentage of vegetation cover variance and community diversity, respectively) suggesting an influence of inter-row vegetation on vine trunk ants.

Although they are considered as generalist predators (Symondson et al., 2002), the role of ants in biological control under temperate and Mediterranean conditions is often underestimated due to their putative negative effect on the crop through mutualistic interactions with aphids and coccids (Beltrà et al., 2017). In tropical regions, ants are widely recognised as natural biocontrol agents, known to regulate pest populations (Philpott and Armbrecht, 2006; Offenberg, 2015). It has been reported that *Solenopsis germinata* preys on eggs and larvae of the Asian corn borer, *Ostrinia furnacalis,* which might reduce pest infestation (Litsinger et al., 2007). Similarly, Sunamura et al. (2020) found that native Japanese ant fauna may increase resistance to *Aromia bungii* attack in Rosaceae trees. The potential of biological pest control by ants requires further investigation and should be considered in the management of vineyards in regions where aphids and coccids do usually not affect vineyards.

4.4. Implications for vineyard management

Winegrowers use the vegetation cover to increase the load-bearing capacity of the soil, allowing machinery use regardless of the rain. Vegetation cover also reduces erosion and runoff. This practice is becoming increasingly common, in line with biodiversity-friendly practices such as organic and biodynamic farming. This nature-based solution is the subject of an increasing number of scientific studies that have highlighted its importance in restoring or improving the multifunctionality of vineyard ecosystems and the ecosystem services they provide (Winter et al., 2018). Our study provides evidence that vegetation cover enhances predation by generalist arthropods in Mediterranean vineyards.

Enhancing the predation function improves vineyard resilience to pest invasion, protecting the crop at the pest arrival stage and decreasing establishment success. Although we did not specifically evaluate the pest regulation service, generalist predators may rapidly and efficiently act as a shield to protect the vineyards from pests such as vine budworms. Because of their high abundance and diversity of foraging strategies, the presence of ants increases the probability of pest detection, which is crucial in pest regulation. The two main predators identified on vineyard plant, *C. vagus* and *C. scutellaris* are active from April to October, which corresponds to that of the two pest insects *L. botrana* and *S. titanus*. They live in colonies of several hundreds to thousands of individuals, and have complementary foraging habits. *Camponotus vagus,* one of the largest ants in Europe (worker size ranges from 6 to 14 mm), which has a solitary to sometimes group foraging strategy is able to attack prey larger than 2 mm. *Crematogaster scutelaris* has smaller workers (approximately 6 mm) and compensate for a size deficit by the number of individuals attacking a prey.

Restoring vegetation cover will also lead to a reduction in herbicide use and/or tillage and may reduce insecticide treatments. However, several constraints still prevent full adoption of vegetated inter-rows, such as competition for water and other resources. In the Mediterranean region, the water stress common during summer limits grapevine growth, yield and grape quality, and thus represents a major factor in the choice, establishment and management of appropriate inter-row vegetation (Celette et al., 2009; Ruiz-Colmenero et al., 2011). Choosing plant species that improve desired ecosystem services and reduce disservices based on plant functional traits is one possible way to address such constraints (Gardarin et al., 2018). To our knowledge, our study is the first to demonstrate the key role of ants in insect predation and the influence of inter-row vegetation on predatory ants in Mediterranean vineyards. Effects on ants should thus be considered in plant species selection and vegetation management.

Authors contribution

C.B., O.B. and C.M. conceived the ideas and designed the experiment; C.B., O.B. and A.B. collected the data; C.B. O.B. and A.M. analysed the data, C.B. and O.B. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Declaration of Competing Interest

The authors report no declarations of interest.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.agee.2021.107327.

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